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Changing Climate Drives Divergent and Nonlinear Shifts in Flowering Phenology across Elevations

Highlights

- Flowering time is diverging among communities across an elevational gradient
- Divergence reflects nonlinear shifts in flowering phenology over three decades
- Climatic variables have also changed differently across space and over time
- Changing climate is driving phenological reshuffling across local spatial gradients

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In Brief

Using 33 years of data, Rafferty et al. test whether flowering times have diverged for neighboring communities comprising 590 species across an elevational gradient. Divergent and nonlinear shifts in flowering time are related to elevation-specific changes in temperature and precipitation and will likely alter species interactions and gene flow.



Changing Climate Drives Divergent and Nonlinear Shifts in Flowering Phenology across Elevations

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SUMMARY

Climate change is known to affect regional weather patterns and phenology; however, we lack understanding of how climate drives phenological change across local spatial gradients. This spatial variation is critical for determining whether subpopulations and metacommunities are changing in unison or diverging in phenology. Divergent responses could reduce synchrony both within species (disrupting gene flow among subpopulations) and among species (disrupting interspecific interactions in communities). We also lack understanding of phenological change in environments where life history events are frequently aseasonal, such as the tropical, arid, and semi-arid ecosystems that cover vast areas. Using a 33-year-long dataset spanning a 1,267-m semi-arid elevational gradient in the southwestern United States, we test whether flowering phenology diverged among subpopulations within species and among five communities comprising 590 species. Applying circular statistics to test for changes in year-round flowering, we show flowering has become earlier for all communities except at the highest elevations. However, flowering times shifted at different rates across elevations likely because of elevation-specific changes in temperature and precipitation, indicating diverging phenologies of neighboring communities. Subpopulations of individual species also diverged at mid-elevation but converged in phenology at high elevation. These changes in flowering phenology among communities and subpopulations are undetectable when data are pooled across the gradient. Furthermore, we show that nonlinear changes in flowering times over the 33-year record are obscured by traditional calculations of long-term trends. These findings reveal greater spatiotemporal complexity in phenological responses than previously recognized and indicate

climate is driving phenological reshuffling across local spatial gradients.

INTRODUCTION

Flowering phenology is a key biological indicator of current climate change [1–5]. However, the magnitude and direction of changes in flowering times appear to vary significantly both among species and among communities, in part because of variation in how much abiotic factors such as temperature and precipitation have changed and in how sensitive species are to those changes [6]. Variation in responses has also been linked to biotic factors. For example, in some communities, flowering phenology responses are related to plant traits, such as flowering season [5], whether species have an annual or perennial life cycle [2,5], and whether species are wind or animal pollinated [5]. In general, species that flower early in the season or are annuals show the greatest advances in phenology, whereas evidence regarding pollination mode is mixed [2,5]. In some cases, closely related species exhibit similar responses; thus, phylogenetic relationships can also be important predictors of shifts in flowering time [7,8].

Altered flowering phenology in response to climate can affect population dynamics and demography via several avenues [9]. For example, plant species that track climate by advancing phenologically have higher metrics of performance such as individual growth [10]. Delayed flowering has been linked to compression of the flowering period and lower fruit and seed set [11]. The timing of flowering in relation to snowmelt and damaging frost events can have large effects on floral abundance in natural populations of wildflowers [12], although consequent floral abortion might not translate into reduced population viability [13]. Nonetheless, phenological responsiveness has been shown to be an important target of natural selection [8]. Increased variability in flowering phenology among species over time has been detected in some temperate datasets [14] and is also likely to have demographic consequences. For example, greater variation in species' flowering times could alter temporal overlap among different species, potentially affecting pollen transfer and seed set.

While communities undergo temporal reshuffling, shifts in flowering phenology can alter interspecific interactions, as



well. For example, earlier flowering can cause asynchrony between plants and pollinators, particularly for species that flower in early spring and are visited by the earliest emerging pollinators, such as queen bumble bees [15]. Experimental manipulations of phenology have demonstrated that flowering time can affect the frequency of both plant-herbivore [16] and plant-pollinator interactions [17,18] and how effectively plants are pollinated ([19], but also see [20]). Over longer timescales, phenological mismatches between plants and pollinators can account for the loss of some interactions and have likely contributed to local species extinctions [21], although in other cases, synchrony between plants and pollinators is maintained under climate change [22]. Indeed, analyses of pollination success over very long timescales could be necessary to determine trends [23]. Competitive and facilitative interactions between plant species are also likely to be reshaped by phenological shifts [24].

Overall, research to date has provided some understanding of what traits predict species-level flowering phenology shifts and how those shifts influence performance, demography, and species interactions. However, how long-term shifts in flowering phenology vary among species-rich communities and subpopulations across semi-arid environmental gradients has not been previously investigated. Prior work on change in flowering phenology across spatial gradients has instead addressed topics such as how shifts in flowering time vary among species [3], across a mosaic of moisture habitats at a single elevation [25], or over only a few years [26]. Ultimately, divergence in flowering phenology among subpopulations (i.e., spatially structured subsets of larger populations) is expected to result in decreased pollen flow and greater reproductive isolation because conspecifics overlap less in flowering time across space [27,28]. Equally, convergence in phenology via increased overlap in flowering time across space could result in increased pollen flow and outbreeding depression if subpopulations are locally adapted [29]. At the metacommunity level, divergent phenological responses among adjacent communities will likely affect trophic and non-trophic interactions, leading to altered community structure and ecosystem processes [30]. For example, if flowering phenology in a montane plant community shifts unevenly across elevations, this will alter the timing of resource availability for species in other trophic levels, such as pollinators, and will likely have downstream effects on seed and fruit production, affecting frugivores, plant recruitment, and competitive interactions. Despite the many possible ways in which climate-change-driven shifts in flowering phenology could affect subpopulations and metacommunities, investigation of these topics is limited by a lack of long-term phenological data across the spatial scales important for maintaining gene flow and species interactions. Without such data, it is impossible to determine whether species are responding at finer spatial scales that could alter the temporal overlap among subpopulations and communities.

Here, we analyze a 33-year record of flowering phenology that spans an elevational gradient of 1,267 m in the southwestern United States that encompasses desert scrub at low elevation, several semi-arid associations (riparian scrub, scrub grassland, oak woodland, and oak-pine woodland), and pine forest at high elevation. This elevational gradient captures a range of environmental conditions that could be indicative of latitudinal

variation in temperature [31], although key abiotic factors vary in different ways along elevational and latitudinal gradients [32]. Our primary goal is to determine whether flowering phenologies of communities and subpopulations are shifting in the same ways across elevations or are responding differently over space. Differential shifts at the community or subpopulation levels would signal changes in temporal overlap or synchrony across elevations. A second goal is to determine whether changing temperature and precipitation patterns are responsible for any community-specific changes in phenology. Since the late 1990s, the study area has been impacted by a long-term warm drought that is characterized by not only precipitation deficits but also rising temperatures, increasing precipitation intensity, and increasing precipitation variability [33–36]. This drought and longer-term climatic changes could be affecting communities and subpopulations along this gradient differently, in part because of species- and population-specific responses and spatial environmental variation that could modulate the changing abiotic conditions. Thus, we seek to determine whether elevational differences in climate variables and their changes over time lead to temporally nonlinear shifts in community-level phenology that could result in spatially divergent phenological changes.

The dataset we analyze is unique; in addition to capturing a steep elevational gradient comprising five communities (defined by elevation bands) with six intergrading vegetative associations, it includes 590 vascular plant taxa ranging from annuals to trees and was collected in a semi-arid ecosystem where precipitation and temperature are key triggers of flowering for many species at low and high elevation, respectively [3,4,37]. There is little overlap in the flowering assemblages of the five communities except in winter [37]. Fifty percent or more of species in each community are highly opportunistic, wherein flowering is triggered by antecedent climatic conditions [38–40]. Because these species have one to several flowering periods of varying durations, and flowering late in one calendar year could be the early part of a flowering season continuing into the next calendar year, we apply circular statistical methods to detect spatiotemporal patterns.

We address the following questions: (1) at the metacommunity level, has flowering phenology diverged or converged across elevations; (2) can variation in temperature and precipitation across elevations explain shifts in flowering phenology; and, (3) within species, has flowering become more, or less, synchronous for subpopulations across space? Our approach reveals spatially divergent, temporally nonlinear changes in flowering phenology among communities and subpopulations that are obscured by the pooling of phenological data across space and the simple linear calculation of long-term trends. These results highlight the utility of circular statistics for detecting patterns in phenology and point to a greater complexity of responses than has previously been recognized, suggesting that climate change will reshuffle communities in multiple dimensions.

RESULTS

Change in Flowering Phenology from 1984–2016

The relationship between flowering time and year varied by elevation band, indicating elevation-specific phenological

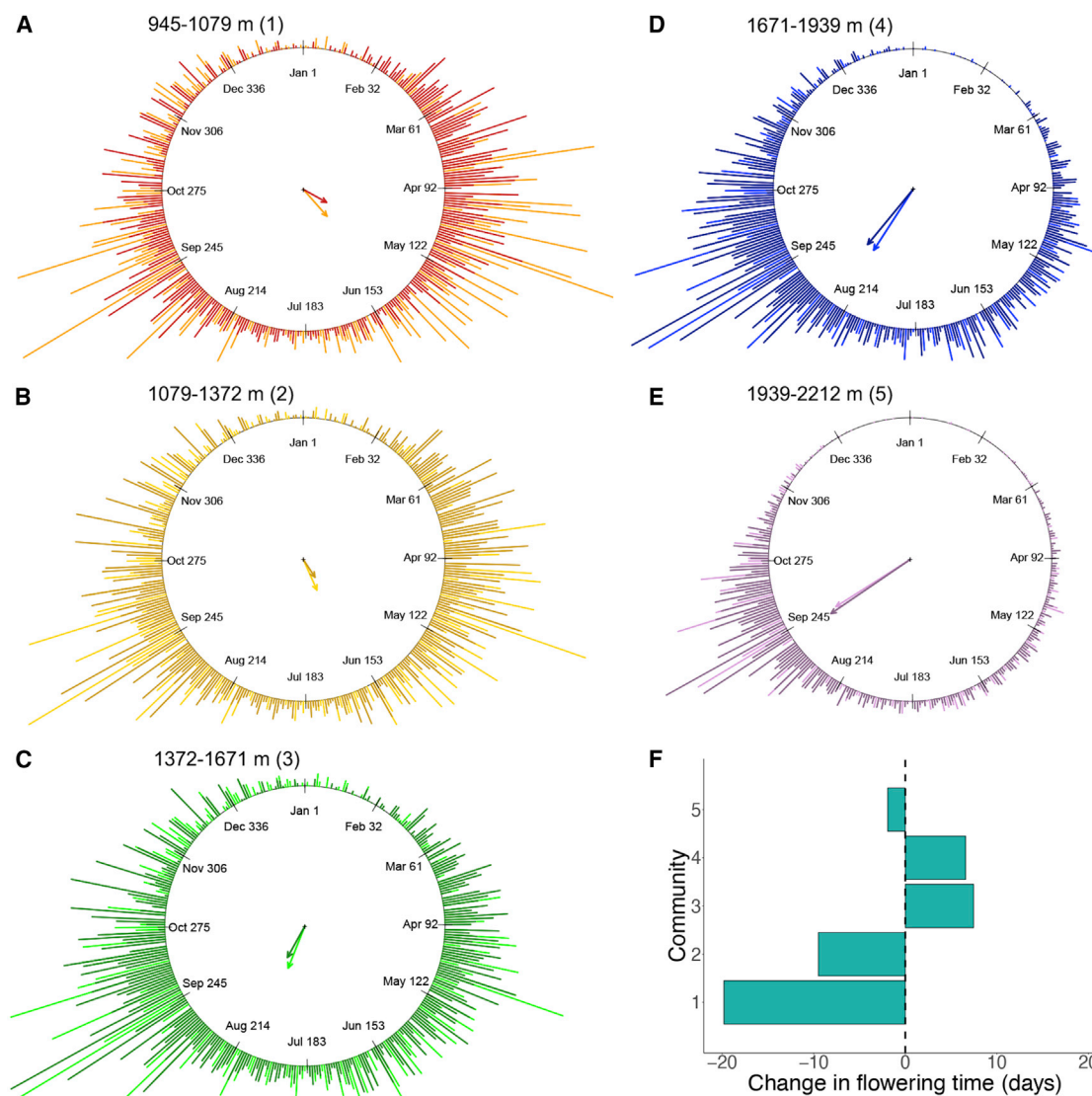


Figure 1. Change in Flowering Phenology of Each Community

(A–E) Circular plots show the dates of flowering, represented by colored lines, for two time periods for all species within each community ascending the transect. Within each circular plot, the lengths of the colored lines indicate the number of phenological observations on each date. The lighter color represents data from 1984–1993, and the darker color represents data from 2007–2016; numbers give the day of year on which each month begins. The arrows show the mean direction and the mean resultant length (a metric of concentration) for a given time period; shorter arrows indicate more dispersed flowering times. (A) 945–1,079 m (community 1); (B) 1,079–1,372 m (community 2); (C) 1,372–1,671 m (community 3); (D) 1,671–1,939 m (community 4); (E) 1,939–2,212 m (community 5).

(F) The summary plot shows the change in flowering time for each community.

See also [Figure S1](#); [Data S1A](#) and [S1B](#).

responses of communities ([Data S1A](#)). We therefore report results per community, numbering communities from 1–5 and ordering from the lowest (1) to highest (5) elevation bands. When examined with linear circular models, from 1984–2016, communities 1–4 shifted significantly earlier at a rate of 2.5, 1.6, 0.44, and 0.36 days per year, respectively, and shifts became smaller with increasing elevation ([Data S2A](#)). However, nonlinear circular models showed that the rate at which flowering advanced accelerated over time for communities 1–4 ([Data S2A](#)). In all cases, nonlinear circular models (with year + year² as predictors) fit better than linear models (with year as the only

predictor; [Data S2B](#)). No significant change in flowering time was detected for the highest-elevation community (5; [Data S2A](#)).

Change in Flowering Phenology from 1984–1993 versus 2007–2016

An examination of changes in flowering time during the first and last decades of the survey period (1984–1993 versus 2007–2016) shows that the two lowest communities (1 and 2, $n = 377$ and 367 species, respectively) exhibited significant advances in flowering phenology of 19.8 and 9.5 days, respectively ([Figures 1A, 1B](#), and [1F](#); [Data S1B](#) and [S2C](#)). In contrast, the two mid-elevation

communities (3 and 4, $n = 364$ and 297 species, respectively) exhibited significant delays in flowering phenology of 7.4 and 6.6 days, respectively (Figures 1C, 1D, and 1F; Data S1B and S2C). Within the highest community (5, $n = 217$ species), flowering time significantly advanced by 1.9 days (Figures 1E and 1F; Data S1B and S2C). Delayed flowering times in communities 3 and 4 in the last decade in relation to the first, in combination with the nonlinear trend toward earlier flowering over the full time series (Data S2A), indicate that flowering times in these communities were even later in the intervening years (1994–2006) than in the most recent decade (Figure S1) and have advanced at a relatively rapid rate in recent years. These shifts in flowering time translate into large differences in the extent to which mean flowering time differed among communities (Figures 2A, 2B, and 2C). For example, the interval between mean flowering dates of the lowest- and the middle-elevation communities (1 and 3) increased by 27 days, almost an entire month, between the first and last decades (Data S2C). Flowering of communities at low to mid-elevations (2 and 3) became significantly less concentrated and more dispersed in time (community 2: $\chi^2_1 = 9.64$, $p < 0.0019$; community 3: $\chi^2_1 = 17.8$, $p < 0.000025$), as depicted by the shorter lengths of the arrows corresponding to 2007–2016 in Figures 1B and 1C.

Change in Temperature and Precipitation

The rate of change in mean daily temperature differed among elevations (significant interaction between year and elevation: $t_{95} = 2.53$, $p < 0.013$), and temperature increased during the survey period (1984–2016) at each elevation (971 m: $R^2 = 0.38$, $F_{1,31} = 18.7$, $p < 0.00015$; 1,379 m: $R^2 = 0.49$, $F_{1,31} = 30.1$, $p < 0.00001$; 1,825 m: $R^2 = 0.58$, $F_{1,31} = 43.3$, $p < 0.00001$; Figure 3A). From the first decade (1984–1993) to the last (2007–2016), mean daily temperature increased by 0.7°C at 957 m (from $19.6^\circ\text{C} \pm 0.14^\circ\text{C}$ [mean \pm SE] to $20.3^\circ\text{C} \pm 0.11^\circ\text{C}$), by 1°C at 1,459 m (from $17.0^\circ\text{C} \pm 0.18^\circ\text{C}$ to $18.0^\circ\text{C} \pm 0.13^\circ\text{C}$), and by 1.3°C at 2,206 m (from $14.4^\circ\text{C} \pm 0.21^\circ\text{C}$ to $15.7^\circ\text{C} \pm 0.14^\circ\text{C}$). Mean daily temperature also increased over the longer term (1930–2016; Figure S2A). In contrast, total annual precipitation decreased during the survey period, and the slopes did not vary among elevations, although the intercepts did (conditional $R^2 = 0.51$, $F_{1,96} = 21.1$, $p < 0.00001$; Figure 3B). There was no significant linear trend in precipitation over the longer term (1930–2016; Figure S2B). However, from the first decade (1984–1993) to the last (2007–2016), total annual precipitation decreased by 26% at 957 m (from 44.4 ± 3.39 cm to 32.8 ± 1.93 cm), by 18% at 1,459 m (from 60.0 ± 4.10 cm to 49.0 ± 3.75 cm), and by 26% at 2,206 m (from 78.4 ± 5.06 cm to 58.3 ± 3.61 cm).

Changing Climate Drives Phenological Change

As described in the STAR Methods, climate variables were calculated for the 12-month window preceding each flowering record. We did not detect temporal autocorrelation within the precipitation or flowering-phenology time series (Ljung-Box tests: $p > 0.05$). Because temperature showed only weakly significant lag-1 autocorrelation (Ljung-Box test: $p = 0.03$), we did not perform any detrending prior to analyses. For all communities, elevation-band-specific increases in temperature were associated with earlier flowering times across the survey period (Table S1). Total 12-month precipitation explained a significant

amount of the variation in flowering time for low-, middle-, and upper-elevation communities (1, 3, and 4); decreased precipitation was associated with later flowering times (Table S1). For communities 3 and 4, we detected significant interactions between temperature and precipitation; flowering is expected to advance more when conditions are both warmer and wetter (Table S1). The magnitudes of the predicted advances in flowering time associated with temperature decrease with increasing elevation. For example, at the mean daily temperature for the lowest community, an increase of 1°C is associated with a 58.3-day advance in flowering phenology, whereas for the highest community, an increase of 1°C is predicted to result in only a 2.25-day advance in flowering (Table S1).

Change in Flowering Synchrony of Subpopulations

Our sample of subpopulations comprised 128 species, 77 of which occur in 4–5 elevation bands. At the subpopulation level, we found significantly reduced synchrony of mean flowering over time for the 67 species in our sample found in both communities 2 and 3. The difference in mean flowering times for subpopulations in these two communities has become 3.26 days larger, growing from 2.52 to 5.66 days (Figure 4; Table S2). In contrast, synchrony significantly increased for subpopulations of the 30 species found in both communities 4 and 5, and mean flowering became 3.90 days closer in time, shrinking from 4.88 to 1.05 days (Figure 4; Table S2). No changes in synchrony were detected for subpopulations found in communities 1 and 2 ($n = 56$ species; Table S2) or 3 and 4 ($n = 40$ species; Table S2).

DISCUSSION

Although climate-change-driven shifts in flowering time have been widely documented, we lack understanding of the spatial variation in shifts within an ecosystem, leaving it unclear whether adjacent communities and subpopulations are shifting in unison or differently. By analyzing long-term phenological data that span an elevational gradient, we show that shifts in community-level flowering time are both spatially divergent and nonlinear over time. Across the entire 33-year time series, all but the highest community shifted toward earlier flowering, but they did so at different rates. Different rates of change occurred not only among different communities but also within communities, some showing accelerated advances in flowering in more recent years. In the first versus the last decades of the time series, communities at lower elevations shifted to flowering several weeks earlier, those at mid-elevations shifted to flowering about a week later, and those at high elevation shifted slightly earlier (Figure 1F). These results demonstrate that traditional calculations of longer-term trends, often made on the basis of comparisons of two time points, can in fact mask more complex, nonlinear changes over time [41,42]. Within species, synchrony in mean flowering phenology has decreased for subpopulations at mid-elevations while increasing for subpopulations at high elevations across the decades (Figure 4). Subpopulations can therefore differ significantly in their phenological responses to changing climate conditions over small spatial scales [26,43], potentially disrupting or augmenting gene flow and influencing local adaptation [27,28,44].

Community-level flowering phenology becomes progressively later with increasing elevation, but the difference in flowering

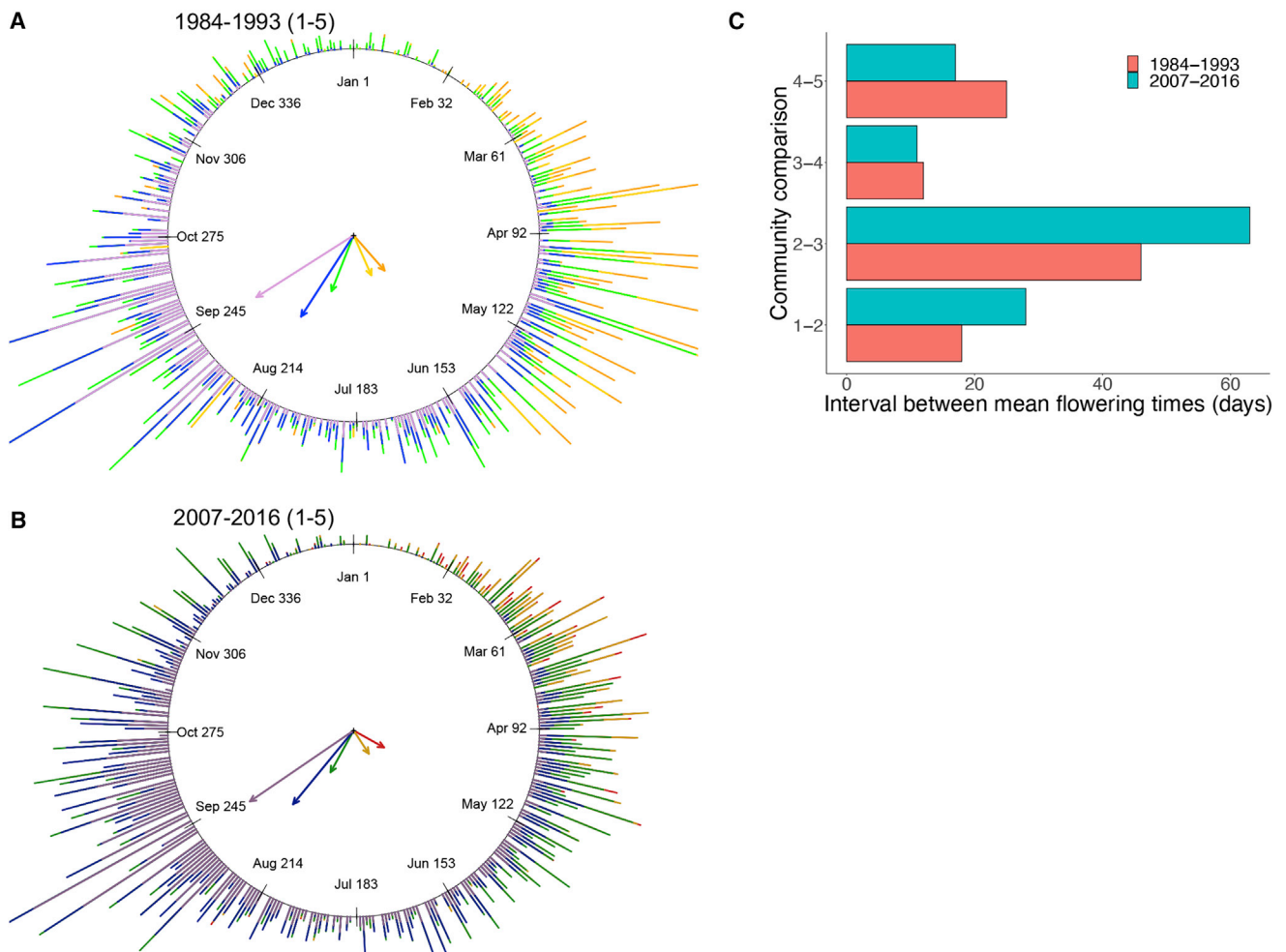


Figure 2. Change in Flowering Phenology of All Communities Comprising the Larger Metacommunity

Circular plots show the dates of flowering, represented by colored lines, for all species in all communities for (A) 1984–1993 and (B) 2007–2016; the summary plot shows the change in the interval between mean flowering times for adjacent communities from 1984–1993 versus 2007–2016 (C). Within each circular plot, the lengths of the colored lines indicate the number of phenological observations on each date. Numbers give the day of year on which each month begins, and the arrows show the mean direction and mean resultant length; shorter arrows indicate more dispersed flowering times.

(A) Orange, 945–1,079 m (community 1); yellow, 1,079–1,372 m (community 2); light green, 1,372–1,671 m (community 3); light blue, 1,671–1,939 m (community 4); pink, 1,939–2,212 m (community 5).

(B) Red, 945–1,079 m (community 1); light orange, 1,079–1,372 m (community 2); dark green, 1,372–1,671 m (community 3); dark blue, 1,671–1,939 m (community 4); purple, 1,939–2,212 m (community 5).

See also [Data S2A–S2C](#).

time between the lower elevation bands grew ten days larger because communities at those elevations shifted at different rates to earlier blooming (Figure 2; [Data S2C](#)). However, there was very little change in the interval between mean flowering dates for the mid-elevation communities, and the difference in flowering time between the highest elevations actually became 8 days smaller (Figure 2; [Data S2C](#)). Reduced differences in the timing of leaf-out were also detected across elevations in the European Alps over six decades [45], and similarly spatially complex shifts are occurring across latitudinal gradients [46]. Flowering times have also become more dispersed across the calendar year for mid-elevation communities (Figures 1B and 1C). Together, these differential responses across space have important implications for patterns of resource availability for

other trophic levels. Even without climate change, this semi-arid environment constitutes a dynamic landscape of floral resource availability that has a relatively low reliability of flowering [47]. Pollinators and other mobile species that forage across the elevational gradient could require behavioral adjustments to maintain temporal overlap with floral resources. The fact that flowering shifted later between the first and last decades in some communities and earlier in others could mean that some pollinators could extend their foraging seasons, which could have important implications for gene flow and reproductive output of plants.

Whether species possess the ability to respond plastically to ongoing climate change or must rely on adaptive evolution is an open question [48–50]. Given overlap in species composition

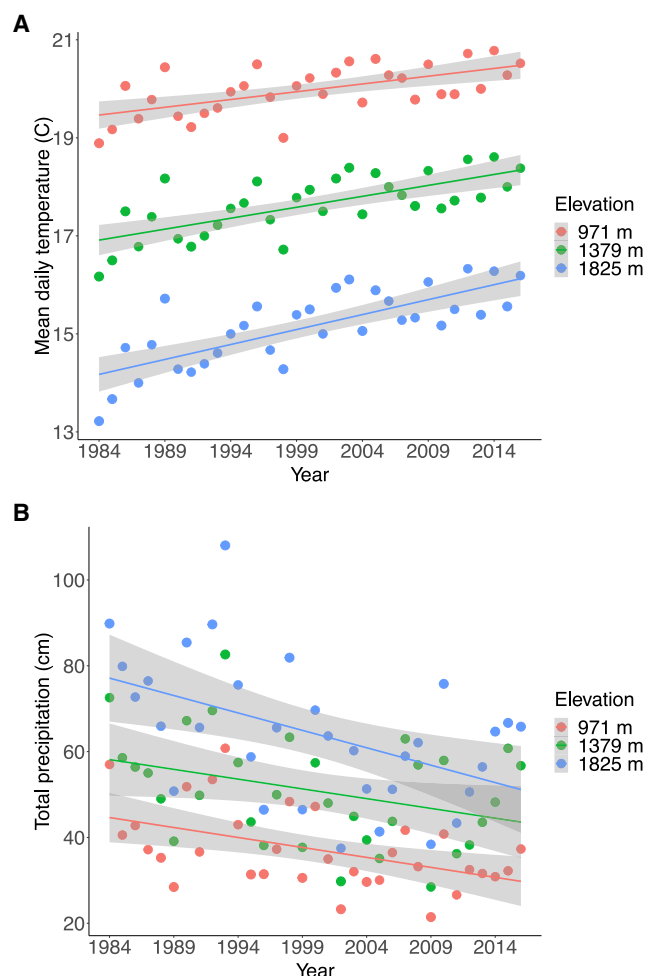


Figure 3. Change in Temperature and Precipitation

(A and B) (A) Significant positive relationships between mean daily temperature and year and (B) significant negative relationships between total annual precipitation and year, partitioned by elevation, for the survey period (1984–2016). In (A), the slopes vary by elevation, whereas in (B), only the intercepts vary by elevation. Confidence intervals (95%) of regression slopes are shown. See also Figure S2 and Table S1.

among communities, with 28% of species spanning four or five elevation bands, our results suggest species can adjust flowering times in response to microclimates that vary across both space and time. In support of the idea that species are tracking elevation-specific microclimates, whether plastically, genetically, or both, the modeled responses to yearly climate variables align with the observed decadal differences in flowering time. For example, the predicted advance of 58 days in mean flowering time per 1°C increase in temperature at the lowest elevation band (Table S1) would generate an advance of 41 days with the 0.7°C increase in temperature that occurred between the first and last decade (Figure 3A). This phenological advance is predicted to be countered by an expected 13-day delay in flowering generated by the 11.6-cm reduction in annual precipitation between the decades (Figure 3B; Table S1), yielding a predicted net advance of 28 days, only 8 days more than the observed advance. The predicted magnitude of the effects of temperature

and precipitation tended to decrease with increasing elevation, as did the magnitude of observed shifts in flowering time. Thus, increasing temperatures and decreasing precipitation appear to be having less impact on communities at high elevation.

By using all observations of flowering for each set of species and years, we avoided biases associated with the use of data on flowering onset alone [51]. Analyses that focus on flowering onset could be particularly problematic in ecosystems where flowering is sporadic or continuous. Although our analyses of subpopulation-level synchrony deal with changes in the mean flowering time, depending on the shape of the flowering curve, changes in the mean will reflect changes in peak flowering time and will likely influence interactions with mutualists and antagonists [52]. Ideally, however, analyses will encompass changes in the entire distributions of flowering, especially when the goal is to predict effects on gene flow. Even with data on the entire flowering record, the tendency for species to flower during both the latter and early parts of the calendar year mean that non-circular analyses will fail to accurately capture the distribution of flowering times. Phenological events cross the calendar-year divide in many ecosystems, particularly those driven by precipitation in addition to temperature, such as the tropical, arid, and semi-arid ecosystems that cover most of the earth's land area [53]. However, our current understanding of phenological responses to climate change is biased toward mid-latitude temperate ecosystems with discrete spring and summer flowering seasons [54]. Circular statistics as employed here provide powerful and underused alternative methods for analyzing phenological datasets [55] and yield novel insight into how phenological distributions are being affected by climate change.

The environmental heterogeneity (*sensu* [56]) of the study area includes dissimilarities in land cover, vegetation, climate, hydrology, and topography both within and among communities. As a result, the mechanisms driving the spatially divergent and temporally nonlinear shifts in flowering phenology are likely to be many and interrelated but are difficult to determine given the paucity of research in semi-arid systems, particularly studies of large numbers of species over elevational gradients. Observational studies over elevational gradients are few [57], and experimental studies might not accurately predict plant phenological responses [58]. Certainly, different species are likely to respond in diverse ways because of variation in sensitivity to changes in temperature and precipitation ([3]; “organismal mechanisms” *sensu* [59]). Thus, the unique composition of species in each community is likely partly responsible for divergent responses. The topography of the study area and the microhabitats inhabited by the species in each community likely also influence the mechanisms involved [32]. Because of differences in exposure, evapotranspiration is likely greater for communities 1 and 2 than communities 3–5. Soils throughout the study area are uniformly shallow lithosoils; organic matter, surface cover, nitrogen content, and acidity tend to increase with elevation [60]. Additionally, coarse talus slopes holding pockets of deeper soils in communities 3 and 4 might retain more water than is possible in the lower two communities, and the highly fractured bedrock could provide water storage in community 5 if refreshed by precipitation [61]. These differences in physical features and evapotranspiration rates (“environmental mechanisms” *sensu* [59]) could explain

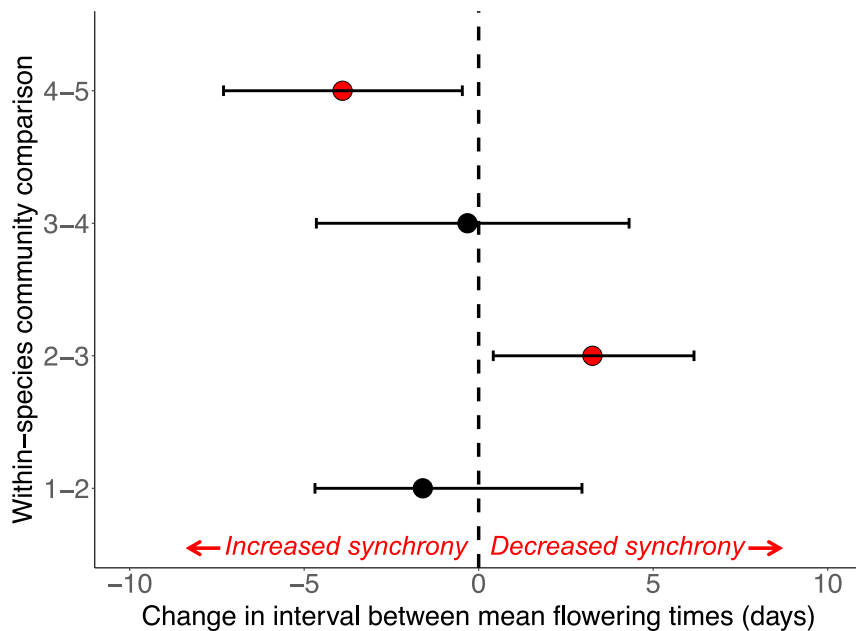


Figure 4. Change in Flowering Synchrony of Subpopulations

Change in the interval between mean flowering times for subpopulations within communities 1 versus 2, 2 versus 3, 3 versus 4, and 4 versus 5 during the first decade (1984–1993) and last decade (2007–2016) of the survey period. Positive values indicate longer intervals (decreased synchrony), and negative values indicate shorter intervals (increased synchrony). The difference in flowering time for subpopulations on elevation band 2 versus 3 was significantly larger in the last decade than in the first, whereas the difference in flowering time for subpopulations on elevation band 4 versus 5 was significantly smaller in the last decade than in the first. Highest posterior density intervals (95%) are shown. See also Table S2.

why flowering shifted at different rates across the gradient, such as communities 1 and 2 shifting earlier at rates 3–7 times faster than did communities 3 and 4. In addition, the responses of communities 3 and 4 were shaped by significant interactions between temperature and precipitation (Table S1), and flowering in those communities advanced more when conditions were both warmer and wetter. Though correlational, this result suggests that these interacting drivers can give rise to divergent phenologies in neighboring communities.

Given the high variability of precipitation and recurring drought in the Southwest [34], it is not surprising that we did not detect a long-term linear trend in total annual precipitation (Figure S2B). However, since the late 1990s, the study area has been impacted by long-term warm hydraulic drought that is characterized by not only precipitation deficits but also rising temperatures [33,34]. The considerable increase in precipitation variability in the Southwest could exacerbate the effects of drought by reducing growth and increasing mortality [35]. In addition, the increasing intensity of monsoon storms [36] will likely result in greater run-off, which means less moisture available to vegetation. In the study area, several dominant species have declined in abundance, particularly *Carnegiea gigantea* (saguaro), *Juniperus deppeana* var. *deppeana* (alligator juniper), *Parkinsonia microphylla* (foothills palo verde), *Pinus discolor* (border pinyon), *Pinus ponderosa* subsp. *brachyptera* (ponderosa pine), and *Quercus arizonica* (Arizona white oak), as have nearly all annuals, particularly when cool-season rains are poor [62]. The result of these declines is likely increased soil temperatures due to an increase in bare ground and decreased cover. These drought conditions could explain some of the temporally nonlinear responses we detected, leading communities 3 and 4 to exhibit delayed flowering in the last decade of the time series in relation to the first.

By virtue of long-term, taxonomically extensive, and highly temporally resolved data that span a spatial gradient, we were able to detect divergent metacommunity-level and subpopulation-level shifts in flowering phenology driven by

changing climatic cues. Our study provides a novel view of how the timing of flowering is changing in a semi-arid ecosystem, an ecosystem type that is expected to expand with continued climate

change [63]. Ephemeral and intermittent stream communities in semi-arid ecosystems contain high biodiversity and provide the same ecological services as do true riparian areas [64]; these systems, and the biodiversity they contain, are highly threatened by climate change [65]. The phenological changes driven by increasing temperature and decreasing precipitation in the xeroriparian habitat in our study system could be indicative of what we can expect elsewhere in the United States, and particularly in the Southwest. This study shows that ecosystem responses to climate change will be both variable and complex, particularly in highly heterogeneous systems characterized by high interannual climatic variability, highly variable topography, and high biodiversity. Short-term studies of only a few species might not show the extent of change occurring, especially when baseline data are lacking, and could in fact produce erroneous conclusions. Our findings demonstrate that communities and subpopulations occupying different microclimates are exhibiting remarkably different responses to changing climatic conditions. The differences in both magnitude and direction of responses highlight how climate change will result in community reshuffling in the temporal dimension.

STAR★METHODS

Detailed methods are provided in the online version of this paper and include the following:

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SUPPLEMENTAL INFORMATION

Supplemental Information can be found online at <https://doi.org/10.1016/j.cub.2019.11.071>.

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AUTHOR CONTRIBUTIONS

C.D.B. collected the data, N.E.R. analyzed the data with input from J.M.D., N.E.R. wrote the first draft of the manuscript, and all authors devised the study questions and edited the manuscript.

DECLARATION OF INTERESTS

The authors declare no competing interests.

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STAR★METHODS

KEY RESOURCES TABLE

REAGENT or RESOURCE	SOURCE	IDENTIFIER
Deposited Data		
Flowering phenology data	This paper; Mendeley data	Mendeley data (https://doi.org/10.17632/k6p34z78x9.1)
Climate data	This paper; Mendeley data	Mendeley data (https://doi.org/10.17632/k6p34z78x9.1)

LEAD CONTACT AND MATERIALS AVAILABILITY

Further information and requests should be directed to and will be fulfilled by the Lead Contact, Nicole Rafferty (nicole.rafferty@ucr.edu). The datasets used in this study have been deposited to Mendeley data (<https://doi.org/10.17632/k6p34z78x9.1>). This study did not generate any new reagents.

EXPERIMENTAL MODEL AND SUBJECT DETAILS

The data come from systematic surveys by one coauthor (CDB) of all plant species and infraspecific taxa (hereafter “species”) in flower along a trail in Finger Rock Canyon ascending to Mt. Kimball in the Santa Catalina Mountains of Arizona, USA (Figure S3). Although the canyon represents less than 1% of the area of the Santa Catalina range, 45% of the known plant taxa in the range have been found there [62]. In 8.05 km, the trail ascends from 945–2212 m, which was partitioned at the beginning of data collection by CDB into five elevation bands that include six vegetative associations in five biotic communities (based on [66]): 1) 945–1079 m (desert scrub, riparian scrub); 2) 1079–1372 m (desert scrub, scrub grassland); 3) 1372–1671 m (scrub grassland, oak woodland); 4) 1671–1939 m (oak-pine woodland); 5) 1939–2212 m (oak-pine woodland, pine forest; Figure S3).

METHOD DETAILS

Phenological Dataset

Every species seen in anthesis (angiosperms) or releasing pollen (gymnosperms), together referred to as “flowering,” was recorded for each community along each 1.6-km-long trail segment on every survey. During the first nine years of data collection, a period characterized by above-normal precipitation, data were collected an average of 30 days per year, with at least two surveys per month during the growing seasons. Subsequently, data were collected an average of 50 days per year, nearly weekly. Because our analyses use all records of flowering and focus on mean flowering dates, this change in sampling frequency should not bias our estimates. Surveys were completed throughout the year with approximately 8% of the total number of surveys being completed each month of the year. The 33-year survey period (1984–2016) considered here comprises 169,030 observations collected during 1,639 surveys. Of the 590 species, 117 were observed in only one community, 140 were observed in two communities, 168 were observed in three communities, 100 were observed in four communities, and 65 were observed in all five communities. Additional details about the data collection protocol and transect can be found in Crimmins et al. [39] and Bertelsen [62]. In particular, Bertelsen [62] gives for each species the years flowering and the number of flowering observations per elevation band and month.

Climate Data

The primary source of climate data was the Parameter-elevation Regressions on Independent Slopes Model (PRISM) database [67], supplemented by on-site rain gauges. Gauges (Tru-Chek) were installed by one of us (CDB) in 2007 to obtain data specific to three locations: at 957 m (near the base of the transect), 1459 m (approximately midway up the transect), and 2206 m (near the peak of the transect). Each gauge was checked on average four times per month during 2007–2012 and 2014–2016, and mineral oil was used to prevent evaporation. Temperature patterns and precipitation data for years the gauge data were not available were extracted from 4 km PRISM cells that include the GPS coordinates of the gauges. PRISM data incorporates factors such as location, elevation, and topography in a climate-elevation regression for each grid cell [68]. Although two of the gauges are located within the same PRISM cell, GPS coordinates within the cell produce different values based on elevation. Monthly PRISM cell and rain gauge precipitation records are highly correlated for each of the three locations ($r = 0.85$ – 0.89). Thus, monthly temperature and precipitation data were extracted for the same approximate elevations as the gauge locations to create three elevation-specific climate predictors of flowering phenology at low-, mid-, and high-elevation. Based on detailed knowledge of the aspect and topography of each elevation band, long-term observation of weather patterns, and vegetation responses to short-term climatic events [see 62], we used low-elevation temperature and precipitation data to represent climate variables for communities 1 and 2, mid-elevation data to represent climate variables for community 3, and high-elevation data to represent climate variables for communities 4 and 5. Briefly, communities 1 and 2 have significant southern exposure, likely resulting in higher evapotranspiration, particularly since precipitation is less than at higher

elevations. Community 3 is situated in the deepest and narrowest portion of the canyon, measured from the top of the ridges forming the canyon to the bottom of the drainage; temperatures are likely moderated by cold air drainage and the largely southwestern exposure. Community 4 has more continuous cover and a largely northwestern exposure, whereas community 5 has considerable cover but with extensive areas of exposed bedrock. The higher precipitation received in communities 3–5, the amount of cover, and exposures would likely lessen evapotranspiration. We regressed mean daily temperature and total annual precipitation against year to test whether these climate variables have changed over the survey period (1984–2016) and since 1930, when a sufficient number of nearby weather stations were available to provide reliable data for the study area [35]. In the initial regression models, we included the interaction between year and elevation to test whether slopes differed by elevation, in which case we fit separate regressions per elevation. If the interaction term was not significant, we fit a linear mixed-effects model with elevation as a random effect to allow intercepts to vary by elevation and compared the fit of models with and without this random effect (conditional versus marginal R^2).

QUANTIFICATION AND STATISTICAL ANALYSIS

Circular Statistics

Data from thirty years were used in the statistical analysis; 2004, 2005, and 2013 were excluded because surveys occurred irregularly during those years. We converted all survey dates to day of year (doy). For all circular statistics, we converted doys to radians and used the R packages “circular” version 0.4-93 [69] and, to construct circular mixed-effects models, “bpnreg” version 1.0.0 [70]. Additional details regarding circular mixed-effects models, their formulation, and interpretation can be found in Cremers and Klugkist [71] and Cremers et al. [72]. Briefly, for the circular mixed-effects models, statistical significance of continuous predictors was gauged by whether the 95% highest posterior density (HPD) lower and upper bounds for circular model coefficients included zero (not significant); significance of categorical variables was judged by whether the 95% HPD intervals for both component I and component II linear coefficients included zero (not significant; [72]). For circular differences between variables, significance was determined by the proportion of iterations that were negative. Models were compared using the deviance information criterion (DIC and DIC_{alt}) and the Watanabe-Akaike information criterion ($WAIC_1$ and $WAIC_2$), which both reward better-fitting models while penalizing model complexity [70]. All analyses were conducted in R version 3.5.2 [73].

Metacommunity Shifts in Flowering Phenology

To examine how flowering phenology at the metacommunity level has changed over time while holding elevation constant, we compared all dates on which flowers of any species were observed within a given community from 1984–2016. This analysis allowed us to determine whether communities within each elevation band exhibited trends of advanced or delayed flowering across all years. We fitted additional models that included a quadratic term for year to test for nonlinear changes in flowering phenology over the full time series. We were also interested in examining trends in the early versus later years of the survey period with the expectation that any phenological changes in response to climate change would be most apparent when comparing the two end segments of the time series. In particular, phenological effects of the drought that began in the late 1990s are likely to be apparent in the latest years of the time series. Therefore, we also examined how flowering time changed per community between the first and last decades of the dataset (i.e., 1984–1993 versus 2007–2016), which additionally enabled us to visualize any shifts with circular plots. Because these analyses use all available flowering records for each community, the various flowering distributions (including any bimodal distributions) are aggregated when mean flowering times are calculated. For each community, we constructed circular mixed-effects models with doys of flowering (in radians) as the response and year (continuous), year + year², or decade (categorical) as the predictor(s), with species identity included as a random effect to account for repeated observations of the same species over time. Year was centered at zero to aid interpretation of model coefficients. We also verified that communities exhibited elevation-band-specific responses in phenology by fitting a circular mixed-effects model with year, elevation band (continuous), and the interaction between year and elevation band as predictors (and species identity as a random effect). The `bpnme()` function within the `bpnreg` package uses a Bayesian approach and Markov chain Monte Carlo (MCMC) samplers to estimate model parameters [71]. For each model, we ran 10,000 iterations with a burn-in period of 1,000 iterations and no lag because there was minimal auto-correlation detected in the MCMC chains. Because the model with the interaction between year and elevation band as a predictor was very computationally intensive, we ran only 1,000 iterations with a burn-in period of 100 iterations for that model. We inspected traceplots to verify that models had converged, which is the method recommended by the package authors [70]. For models with continuous predictors, we report the ‘slope at the mean’ (SAM) circular model coefficients because they are the least biased [72]. To test whether the concentration of flowering times (i.e., the spread of flowering times throughout the calendar year) changed for a given community between decades, we used Wallraff’s test for a common concentration [74].

Climate Models

To test whether climate variables were related to observed shifts in flowering time within each community, we used circular mixed-effects models with doys of flowering as the response and mean daily temperature and total precipitation during the 12-month window preceding and including the month in which flowering was observed as predictors, with species identity as a random effect. In our initial models, we also included the interaction between temperature and precipitation. These climate variables are specific to each flowering record and capture temperature and precipitation conditions for a one-year period before each observation, regardless of the calendar date of flowering. To test for temporal autocorrelation within each time series (precipitation, temperature, and flowering

phenology), we used Ljung-Box tests with a lag of one year [75]. Temperature and precipitation variables were centered at zero to aid interpretation of model coefficients. As before, we ran 10,000 iterations per model with a burn-in period of 1,000 iterations and no lag because there was minimal auto-correlation detected in the MCMC chains. We inspected traceplots to verify that MCMC chains had converged [70]. For these models, we report the SAM circular model coefficients [72].

Subpopulation Changes in Flowering Synchrony

To analyze within-species shifts in flowering phenology across time and space, we limited the dataset to only those species that: (i) occurred in at least two adjacent communities along the transect (i.e., communities 1 and 2; communities 2 and 3; communities 3 and 4; communities 4 and 5), (ii) had been observed flowering during at least four years in the first decade (1984–1993) and four years in the last decade (2007–2016), and (iii) had been observed at least four times per community in each year flowering was documented. The resulting dataset comprised 128 unique species with subpopulations in two or more adjacent communities. We then calculated the mean day of flowering (in radians) per species per community per decade and took the difference between these means for each community per decade (e.g., we subtracted the mean day of flowering for a given species in community 2 in the first decade from the mean day of flowering for the same species in community 1 in the first decade; we repeated this process for the last decade). These values indicate how much the mean flowering times of subpopulations differed in the first versus the last decade of the dataset and provide a way to test for changes in subpopulation-level synchrony. These differences were first converted back to a circular variable so that values corresponded to the number of days in radians on the unit circle, measuring counterclockwise from 0 radians if the differences were positive and clockwise from 2π radians if the differences were negative. We then used these differences as our response variable in circular mixed-effects models with decade as the predictor and species identity as a random effect. We used the same model specifications as in previous models.

DATA AND CODE AVAILABILITY

The phenology and climate datasets used in this study are available at Mendeley data (<https://doi.org/10.17632/k6p34z78x9.1>).